Pg-11 - "Tables records the range of differences that is expressed among presently isolated state of AIM-1

Table-2

Phenotypes of kernels appearing on ears of plants having constitutions entered in column 2 when pollen of plants homozygous for a_1^m, sh_2, and y and having no Spm was placed on silks of these ears.

	Constitution of pistillate parent.			no. of plants	Phenotype of Kernel: uniformly pigmented (no Spm) Y	y	spots of deep pigment in colorless/or light (Spm) Y	y	Total
A	a_1sh_2/a_1sh_2;	Y Spm/	y +	13	813	1467	1386	815	4481
B	" "	Y/y;	1 Spm	2	96	97	126	116	435
C	" "	y/y;	1 Spm	6	—	1260	—	1216	2476
D	$a_1^m sh_2/a_1sh_2$;	Y Spm/	y +	15	665	1156	1080	638	3539
E	" "	; Y/y;	1 Spm	1	43	47	31	35	156
F	" "	"	2 Spm	1	45	58	119	115	369
G-1	" "	Y Spm/y +	main ear	1	40	74	71	41	226
G-2	" "	Y/y;	1 Spm. Tiller		122	129	144	121	516
H	" "	y/y	1 Spm	8	—	864	—	852	1716
I	a_1sh_2/a_1sh_2	Y Spm/	y +	30	1366	2619	2472	1335	7792
J	" "	y/y	1 Spm	17	—	3465	—	3281	6746
K	" "	Y/y	1 Spm	4	477	500	455	462	1894
L	" "	"	Spm/Spm	2	3	4	259	281	547
m	" "	"	1 Spm	15	1536	1664	1544	1654	6398
n	$a_1^{m-1} sh_2/a_1sh_2$	Y Spm/	y + (?)	1	68	92	82	61	303
O	"	" Y/y	2 Spm	1	82	75	203	201	561
P	"	" Y Spm/	y +	7	581	713	628	543	2466
Q	" "	Y/y	2 Spm	1	51	71	170	175	467
R	" "	Y/y	3 Spm	1	16	15	95	110	236
S-1	a_1sh_2/a_1sh_2	Y Spm/	y + (main ear)	1	67	130	141	78	416
S-2	" "	"	" (tiller ear)		60	140	122	91	413

Tables

$a_1^{m1}\ sh_2 / a_1 sh_2 ; Y/y$ ♀ × $a_1 sh_2 / a_1 sh_2 ; y y ;$ no Spm ♂

	Phenotype of Kernel												
	Dark colored aleurone				Spots of deep color in colorless background				Colorless aleurone				
	Sh2		sh2		Sh2		sh2		Sh2		sh2		
...er in culture A. Y Spm/y + Plant no.	Y	y	Y	y	Y	y	Y	y	Y	y	Y	y	Total
6629 A-1	69	112	0	0	117	71	1	1	1	0	186	187	745
" A-3	34	52	0	1	43	37	1	0	0	0	85	83	336
" A-4	23	65	0	0	56	36	0	0	0	0	90	84	354
" A-6	34	67	0	0	78	37	1	0	0	0	86	113	416
" A-7	29	59	0	0	58	36	0	0	4	1	105	100	392
" A-9	80	99	1	1	99	72	0	0	0	1	158	205	716
Totals	269	454	1	2	451	289	3	1	5	2	710	772	2959
Derivation of progeny plants total ... Spm	35	28		2	43[1] (1 pale)	23	3				56	60	250
B. Y Spm Spm/y + +													
6629 A-8	19	56[4]	0	0	66	53[21]	0	0	0	0	101[12]	87[13]	382
C. Y Spm/y + plus 2 Spm													
6629 A-2	10	27	0	0	123[19]	118[10]	0	2	1	0	128[20]	116[11]	525
D. Y/y plus 2 Spm													
6629 A-5	45[10]	52[9]	0	0	122[13]	122[10]	1[1]	0	0	0	188[29]	154[33]	684

Table 4

A. $a_1\ sh_2 / a_1\ sh_2$; 1 Spm ♀ × $a_1^{m1}\ Sh_2 / a_1^{m1}\ Sh_2$ (state 5718); no Spm ♂

Phenotype of kernels.

Plant number of ♀	uniformly lightly pale	Dots of deep pigmentation in colorless background.	Total
6861-1	229	174	403
6861-7	139	148	287

B. $a_1^{m1}\ Sh_2 / a_1^{m1}\ Sh_2$ (state 5719A-1) ♀ no Spm × 6861-1 and 6861-7: $a_1\ sh_2 / a_1\ sh_2$; 1 Spm ♂

Phenotype of kernels.

number of ♀♀ tested	♂ parent	uniform dark pale	areas of deep pigmentation in colorless background	Total
4	6861-1	788	779	1567
5	6861-7	988	988	1976

C. $a_1^{m1}\ Sh_2$ (state 5720) $/ a_1\ sh_2$ no Spm ♀ × $a_1\ sh_2 / a_1\ sh_2$ 1 Spm (plants 6861-1 or 6861-7) ♂ and $a_1\ sh_2 / a_1\ sh_2$ no Spm ♂

Phenotype of Kernels

♀♀ tested	♂	Colorless		areas of light pigmentation in colorless background		Totals
		Sh_2	sh_2	Sh_2	sh_2	
6 plants	6861-1	530	951	445	0	1926
5 of above 6 plants	$a_1\ sh_2 / a_1\ sh_2$; no Spm	741	795	0	0	1536
10 plants	6861-7	886	1671	798	1	3356
8 of above 10 plants	$a_1\ sh_2 / a_1\ sh_2$; no Spm	1157	1177	0	0	2334

Stability of mutants produced by a_1^{m-1}

Mutation producing events may occur at a_1^{m-1} not only in somatic cells of the plant and in the endosperm cells of the kernel, but also in ancestor cells of the gametes, that is, in the sporogenous or gametophytic cells. The frequency of their occurrence in these latter cells, and the phenotypic expression that will result from this, is related directly to the state of the a_1^{m-1} locus itself (see table 1). With most states, the majority of germinal mutations modify the locus in such a way that it is subsequently capable of acting much like the standard A_1 locus. However, all states give rise to some germinal mutations that express a much reduced capacity for pigment production. State -, (5720) figure 1, produces almost exclusively this latter type of mutant. When plants carrying a_1^{m-1} and Spm are crossed by plants that are homozygous for a_1, some kernels on the resulting ear may exhibit a modified phenotype and this is often the consequence of a germinal mutation at a_1^{m-1}. ~~These~~ Such kernels are uniformly pigmented and the intensity of this usually differs markedly from that appearing in the kernels having an unmodified a_1^{m-1} locus and no Spm. Some kernels exhibiting these phenotypes e~~xpected from germinal mutations~~ were removed from ~~some of the~~ ears, and the plants grown from them were examined for anthocyanin distribution and was tested for presence or absence of Spm. It was found that ~~the intensity~~

these kernels gave rise to plants that were uniformly pigmented. When, in turn, they ~~plants~~ were crossed by plants that were homozygous for a_1^{m-1} but had no Spm, it was learned that Spm was present in some of them and absent in others. However, in all tests ~~cases~~, the phenotype produced by the mutated locus was the same in all kernels carrying it. In other words, the action of the locus was ~~remained unchanged and segregated quite normally on these ears.~~ not altered by the presence of Spm. These plants were also crossed by plants carrying Spm and from this test it was learned that the mutant locus in those plants that had no Spm would also remain unaltered in expression when Spm was introduced.

The most graphic illustration of stability of mutants in the presence of Spm is derived from crosses of plants carrying the state of a_1^{m-1} (5720) that produces no anthocyanin in the absence of Spm but gives rise to many early occurring mutations to low alleles of A_1 in its presence. When this state is present, the frequency of occurrence of germinal mutations is high, and they are revealed by the appearance of kernels exhibiting a uniform distribution of pigment over the aleurone layer. The intensity of this pigment among the different kernels having germinal mutants varies from very faint in some to rather dark pale in others. The same range in intensity of pigmentation is expressed in the plants grown from these kernels, and the degree of this corresponds ~~ing~~ with that ~~shown~~ shown by the kernel from which the plant arose. These plants, in turn, were crossed with ~~the~~ an Spm tester stocks (homozygous for a_1^{m1}, and having no Spm) in order to determine the presence or absence of Spm in them, ~~and~~ Spm was found to be present in some of them. The stability of the mutant in the presence of Spm was clearly revealed in this test cross. Some of the ~~xxxx~~ ear resulting from this cross ~~carried~~ received the mutated locus and Spm ~~derived~~ from one parent and the a_1^{m-1} locus ~~derived~~ from the other parent. ~~In~~ These kernels exhibited spots of deep pigmentation in a uniformly pale colored background, figure 3. The deeply pigmented spots represent Spm induced mutations at the a_1^{m-1} locus contributed by the tester stock. The lightly pigmented background in which these appear reflects the action of the mutated locus contributed by the other parent, ~~which is~~ obviously its expression is unaffected by ~~stable in~~ the presence of Spm.

Types of Spm elements

The phenotypic expression of a_1^{m-1} produced by ~~of~~ the Spm element, considered in the previous sections, was remarkably constant and predictable, notwithstanding the many different locations of it and changes in these that ~~were determined~~ were detected. However, Spm elements with modified types of ~~expression~~ action have appeared and the origin and expression of one type will be considered here. Occasinnally, on the ear of an a_1^{m-1}, Spm carrying plant, a kernel ~~with~~ exhibiting an aberrant phenotype ~~expression~~ will appear, and one type has appeared rather frequently. Instead of showing a number of deeply pigmented spots in a colorless background, such kernels show only a tiny spot or several such spots in a colorless background. Plants ~~have been~~ were grown from several such kernels and they and their progeny were tested to determine the ~~cause of~~ reason for the altered phenotypic expression. These tests have shown that in ~~such~~ some of these kernels, an Spm-type element is present but its capacity to suppress gene action at a_1^{m-1} and to induce mutations at this locus is much weakened. It has therefore been symbolized as Spm-w, ~~in contrast to the standard Spm element involved in the tests previously described~~.
In this section, the standard Spm element will be designated Spm-s to distinguish it from the Spm-w element.

Spm-w elements have been located in several different chromosomes. The one which will be considered ~~here arose in~~ have appeared in a single kernel on an ear produced by a plant carrying Spm-s in chromosome 5. This plant was a_1^{m-1} Sh_2 (state -, figure 1) / a_1 sh_2, Pr-/pr Spm-s, y/y, wx/wx in constitution, was crossed by a plant that was homozygous for a_1, sh_2, y, Pr, and Wx and had no Spm. On the resulting ear there were 87 uniformly pigmented Sh_2 kernels, (no Spm) 103 Sh_2 kernels that had a number of deeply pigmented spots in a colorless background, (Spm-s present) and an [illegible] Sh_2 kernel~~s~~ that showed only several small dots of deep pigment in a colorless background. In addition, there were 186 sh_2 kernels that were totally colorless. Progeny was grown from ~~all~~ the 3 expected classes of kernels ~~and~~ and from the kernel with the aberrant [illegible]. Each plant was tested for presence or absence of Spm. From such tests it was possible to learn of the presence of Spm-s in the pr carrying chromosome of the variegated parent plant. ~~Both~~ The plant~~s~~ derived from the Sh_2 kernel~~s~~ that showed only several tiny spots of deep pigment in a colorless background ~~were~~ was uniformly pigmented and in this respect, ~~they~~ it resembled the plants that had no Spm. Two ears of ~~one of these~~ this plant~~s~~ were used in test crosses. Pollen from a plant homozygous for a_1, sh_2, y, pr, and Wx and having no Spm was used on the silks of one ear, and pollen of a plant that was Y/y but homozygous for a_1^{m-1} (state-, figure 1), Sh_2, pr, and wx and having no Spm was used on silks of the second ear. The kernel types on the~~se~~ resulting ears indicated that the constitution of the tested plant was a_1^{m-1} Sh_2/a_1 sh_2, Wx/wx, Pr/Pr, y/y. However, kernels exhibiting the same phenotype as that from which the plant arose segregated on each of these ears. Among the 328 kernels appearing on the ear produced by the latter cross, 169 were uniformly pigmented (no ^{S}pm type), and 78 of these were Wx and 91 wx. There were 118 kernels that had the same phenotype as that from which the parent plant arose (57 Wx : 51 wx) and in addition, there were 51 totally colorless kernels (27Wx: 24 wx). In order to determine the factors responsible for the modified type of expression of a_1^{m-1}, plants were grown from ~~all~~ Y kernels in each of these 3 classes ~~of kernels~~ on this ear ~~and those carrying Y, delivered by the male parent, were selected~~. At maturity, the phenotypes of the plants derived from all three classes of kernels were ~~alike~~ similar in that each was uniformly pigmented. However, the plants derived from the colorless kernels, or those that [illegible] in a colorless background developed pigment very slowly, in contrast to the plants derived from the pale kernels which developed pigment rapidly. The silks of an ear of each of these plants received pollen from a plant that was homozygous for a_1, sh_2, y, and had 1 ^{S}pm-s element, closely linked with y in one of its two chromosomes 6. Some of these pollen parents were Pr/pr and others were pr/pr. From these tests it was concluded that action of the a_1^{m-1} locus had not been altered but that an Spm ~~like~~ element with much ~~xxxxxx~~ weakened action ~~was present~~ in ~~one chromosome 5~~ each of the plants derived from the kernels that were eaither ~~totally~~ colorless or showed only 1 or several small spots of deep color in a colorless background, and that this element was absent in the plants derived from the uniformly colored kernels. The reason for this conclusion is evident from the types of kernels that appeared on the test-cross ears that these plants produced, as shown in table (a). Those entered in A of this table are from ears of plants derived from the uniformly colored kernels. Those entered in B ~~of this table~~ are ~~d~~ from ears of plants derived from the totally colorless kernels or those in which only 1 or several small spot deep color appeared. Only two classes of a_1^{m-1} carrying kernels appeared on the ears of plants entered in A ~~of the table.~~ Half of them were uniformly dark pale in color (no Spm) and half exhibited many spots of deep pigmentation in a colorless background (Spm-s present). On the other hand, the a_1^{m-1} carrying kernels on ears produced by plants entered in B of this table fell into four classes. Half of them (1323 kernels) exhibited the typical pattern of variegation produced when Spm-s is present. A quarter of them (629 kernels) were uniformly dark pale in color (no Spm). The remaining quater (693 kernels) showed either a few dots of deep pigmentation in a colorless background (524 kernels) or they were totally colorless (169 kernels). In some of the crosses entered in this table, the male parent was pr/pr and when these plants were used ~~as pollen parent~~ in the crosses entered in B, of table (a), the distribution of Pr to pr among the three classes of a_1^{m-1} Sh_2 carrying kernels indicated the presence in the pistillate parent of a factor, carried in the pr chromosome, that is responsible for the ~~phenotype~~ colorless kernels exhibiting very few or no A_1 dots. These ratios, of Pr to pr in each of the 4 a_1 m-1 classes exhibiting pigment, ~~are~~ is entered at the foot of B of table (a). The ratios ~~also~~ indicated that the Spm-s element, introduced by the pollen parent, was epistatic to th~~is~~e ~~factor.~~ Spm-w element. One of the plants belonging to group B of table (a) had been crossed by a plant homozygous for a_1^{m-1} Sh_2, y, and pr and having no Spm. The types of kernels this cross produced also indicated the presence of the weakened Spm-type factor that was carried in the pr chromosome. There were 253 uniformly pigmented kernels of which 70 were Pr and 183 were pr; 146 kernels showed 1 or several small A_1 dots in a colorless background and 112 of these were Pr and 34 were pr. In addition, there were 69 totally colorless kernels.

Another series of progeny tests were conduced with plants derived from the several classes of kernels on the ear just described and also from kernels entered in B of table (a). These progeny tests confirmed the conclusions derived from the tests just described. Details regarding these tests will not be ~~given~~ reviewed here but in order to indicate the obviousness of the conclusions, data from test crosses of some of these plants are given in table (b).

It was learned from these studies that the Spm-w element behaved as a weakened Spm element both with regard to suppression of pigment formation at a_1^{m-1} and with regard to mutation producing capacity. When it is present, the plants having a_1^{m-1} develop pigment but the rate of this is very much slower than in the a_1^{m-1} plants that have no Spm element. Also, suppression of pigment formation in the kernel is not always complete for a very coloration may appear at the base of some of the kernels that have Spm-w. In order to determine if the Spm-w element has a weakened capacity to induce mutations, it was incorporated into plants having various different states of a_1^{m-1} but no Spm-s. These tests indicated that the presence of Spm-w results in a marked reduction of the frequency of occurrence of mutation but does not alter the time of their occurence. This latter remains a function of the state of the a_1^{m-1} locus.

Although Spm-w elements residing in different chromosomes of the complement have been detected, no certain evidence of transposition of this element has yet been obtained. Tests of this are not extensive, however, and thus no conclusions regarding this may yet be drawn. The origins of Spm-w elements from modifications of Spm-s elements is to be suspected but this conclusion could only be considered as tentative since evidence in support of it is limited to the two cases that were adequately examined. In each of these two cases, however, the ~~where~~ Spm-w elements appeared in the same chromosome of the complement that had carried Spm-s, and it showed the same linkage relations with a genetic factor in this chromosome as Spm-s had shown.

(pm. 10) Table

6888

$a_1^{m1} Sh_2 / a_1^{m1} Sh_2$ or $a_1^{m1} Sh_2 / a_1 sh_2$ ♀ × $a_1 sh_2 / a_1 sh_2$ 1 Spm ♂ y/y
Pr/pr Y/y Pr/pr or pr/pr

A. Plants From pale kernels.

Plant	Constitution		Sh_2: uniform pale	many A_1 of dark colored	few A_1 dots in colorless background	Totally colorless	sh_2: colorless sh_2	$a_1 \to A_1$ sh_2	Totals
A-3	$a_1^{m1} Sh_2$	$a_1^{m1} Sh_2$	214	183	0	0	—	—	397
B-1	"	"	205	288	1	0	—	—	494
A-1	"	$a_1 sh_2$	121	136	1	0	288	0	546
A-4	"	"	108	102	0	0	189	0	399
A-5	"	"	113	121	0	0	200	0	434
B-2	"	"	134	147	0	0	257	0	538
B-3	"	"	120	91	0	1	208	0	420
Totals			1015	1068	2	1			

B. plants From colorless, or rare A_1 dots or tot all colorless

Plant	Constitution		uniform pale	many A_1	few A_1 dots	Totally colorless	colorless sh_2	$a_1 \to A_1$ sh_2	Totals
C-3 I+II	$a_1^{m1} Sh_2$	$a_1^{m1} Sh_2$	131	261	82	69	—		543
D-1	"	"	137	274	117	20	—		548
C-4	"	"	91	249	95	39	—		474
C-2	$a_1^{m1} Sh_2$	$a_1 sh_2$	54	122	48	4	217	1	441
C-5 I+II	"	"	91	145	69	13	313	2	633
D-3	"	"	68	139	72	4	264	0	547
D-6	"	"	57	133	41	20	244	0	495
Totals			629	1323	524	169			
Totals from ♂ I+II			447	886	383				

176 Pr : 271 pr; 453 Pr : 433 pr; 260 Pr : 123 pr

Female ... A_1 dot ♀ × $a_1^{m1} Sh_2$ pr no Spm ♂

Plant	uniform pale	many A_1	few A_1 dots	Totally colorless
D-2	253	0	146	69

70 Pr : 183 pr; 112 Pr : 34 pr

4 plants test cf
8 " from ...

Selections for test mg:

6888C-3^I a, m1 sh2 / a, m1 sh2 Pr Spm-w / pr+ Y/y × a1 sh2 pr
[Culture 7262] y Spm/y+

" C-3^II " " " " " × a1 sh2 Pr/pr
[culture 7263] y Spm/y+.

6888 D-2 a, m1 sh2 / a, m1 sh2 Pr Spm-w / pr+ Y y × a, m1 sh2 pr y wx
[Culture 7264] no Spm; no Spm-w

Origin -

6629B-(5)^I × Bollinger 1040 (1) [1953]
a, m1 sh2 / a, sh2 a2 sh2 y Pr/Pr
Pr+ / pr Spm-w y y

Colorless, few A1 dots Pr y = 6683 B (2) [1954]

6683B (2) × 6641A-5
a, m1 sh2 / a1 sh2 a, m1 sh2 / a, m1 sh2 pr pr wx
Pr+ / Pr Spm-w Y/y no Spm.
y y

gave 6888 culture [1955]

Table (2)

7264

I $a_1^{m1} sh_2 / a_1^{m1} sh_2$; Pr Spm-w / pr + × $a_1^{m1} sh_2 / a_1^{m1} sh_2$; pr/pr no Spm

7262

II " " " × $a_1 sh_2 / a_1 sh_2$; pr/pr, y Spm-s / y+

7263

III " " " " × " " ; Pr/pr " "

A. Plants from dark pale kernels. I = 5, III = 10 } Total = 15. no Spm-s; no Spm-w

B. Plants from colorless kernels with 1 or several A_1 dots. Pr ♀ × $a_1^{m1} sh_2$ y pr no Spm ♂

Phenotype of Kernel

No. of plants tested		Constitution of tested plant	uniform dark pale		colorless with 1 or several A_1 dots		Colorless	Totals
			Pr	pr	Pr	pr		
I	9	Pr Spm-w / pr +	431	1207	702	232	602	3174
II	5	Pr Spm-w / pr +	206	769	437	116	390	1918
III	5	Pr Spm-w / pr +	298	782	403	138	457	2078
Totals		" "	935 25.3%	2758	1542	486 23.9%	1448	7170
III	2	Pr + / pr-Spm-w		203	124	229	323	1354
IV	2	Pr/Pr Spm-w	284	—	143	—	142	569

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7263C-5, C-7

C Plants from kernels with many deep colored spots in colorless background (Spm-o), Y, Pr.

	Spm-o: many spots of deep color in colorless background				Spm-w; no Spm-o: 1 or several small dots of color in colorless background				Spm-w: Colorless		no Spm-S, no " w: uniformly dark pale				Total
	Y		y		Y		y				Y		y		
	Pr	pr	Pr	pr	Pr	pr	Pr	pr	Y	y	Pr	pr	Pr	pr	
II 3 Y+/y Spm-o; III 1 Pr Spm-w/pr+	16	19	360	342	212	69	11	9	56	5	98	200	9	12	1418
II 1 Y+/y Spm-o; III 4 Pr/pr no Spm-w	31	33	300	287	0	0	0	0	0	0	287	233	47	51	1268
III 1 Y/y; 1 Spm-o (Pr Spm-w/pr +)	30	45	48	30	20	5	11	5	19	18	* 22	20	* 15	22	310
III 1 Y+/y Spm-o Pr/Pr no Spm-w	8	—	60	—	0	—	0	—	0	0	67	—	16	—	151
III 1 Y/y 3 Spm-o (Pr Spm-w/pr+)	98	54	97	96	3	4	0	0	6	1	13	25	1	1	399
III 1 Y+/y Spm+/Spm-o Pr/Pr no Spm-w	81	—	194	—	0	—	0	—	0	0	135	—	28	—	438

D. Plants from kernels with many deep colored spots in colorless background; y; Pr × 9, m1 sh2 y pr no Spm-o; no Spm-w 07

			Pr	pr			Pr	pr					Pr	pr	
III 2 1 Spm-o Pr Spm-w/pr+			97	102			45	18		24			34	72	392
III 1 2 Spm-o " "			183	217			30	11		20			20	51	532
III 2 1 Spm-o Pr/pr no Spm-w			121	126			0	0		0			130	134	511
III 1 2 Spm-o " " "			162	135			0	0		0			50	57	404
III 1 1 Spm Pr/Pr " "			204	—			0	—		0			206	—	410

* different Pr + including in pale class.
[illegible - [illegible]]

Modifier element in the Spm system

In the course of a test undertaken to examine Spm number and location in the progeny of a plant carrying two Spm elements, both located in one chromosome 5, a kernel appeared on ~~an~~ one ear of a ~~single~~ plant in which the frequency of mutation at a_1^{m-1} was greatly augmented. Subsequent tests of the plant derived from this kernel and its progeny indicated the presence of an element, belonging to the Spm system, that increases the frequency of occurrence of mutation at a_1^{m-1} and with each of five tested states of At, but does not alter the time during ~~the~~ development when

however, Its presence may be detected only when Spm also is present.

these will occur. / Like Spm, it may undergo transposition. In all essential respects, it acts like a complementary controlling element within the Spm system.

The kernel carrying the modifier element appeared on ~~the~~ one of two ears of a plant that was a_1^{m-1} Sh_2/a_1 sh_2, Pr/Pr, Wx/Wx ~~in constitution~~ two ~~of its ears~~ when/each ear ~~it~~ had been used in a cross with a plant that was homozygous for a_1, sh_2 pr, and Wx and had no Spm. / On these ears, there were 167 uniformly dark pale colored kernels in the Sh_2 class (no Spm), 186 Sh_2 kernels with spots of deep color in a colorless background (Spm present) with a pattern of mutant spots similar to that for it carried this state of a1 m-1.

shown in 7 of figure 1. There were also 384 colorless, sh_2 kernels.

In addition, on one of these ~~two~~ ears, a single Sh_2 kernel appeared that exhibited a very marked increase in the number of pigmented spots. ~~This kernel was removed and~~ the plant grown from ~~it~~ this kernel also exhibited a very high rate of mutation at a_1^{m-1} in its somatic cells. In order to examine the nature of the modification that was responsible for this marked increase in frequency of mutation, one ear of this plant, (number 6889), was self-pollinated. Another ear received pollen from a plant that was homozygous for a_1^{m-1} (state), Sh_2, pr, and wx. The reciprocal cross was also made. In addition, pollen from plant 6889 was placed on the silks of ~~tops of~~ two plants that were homozygous for a_1^m sh_2, pr, and had not Spm. The kernel types and the ratios of them that appeared on the ears produced by these crosses indicated the presence of one Spm element in plant 6889 but it was not linked with Pr. Among the variegated kernels, there were two classes. In one, the kernels exhibited the expected number of mutant spots. In the other, one the other hand, the number of these spots was greatly increased. The ratios of these two types of variegated kernels suggested the presence in plant 6889 of an independently located modifer element that serves to increase the frequency of mutation at a_1^{m-1} and does so either with state 5719A-1 or state 5719. In order to verify this, kernels were selected from the various classes ~~and~~ on these ears, and the plants grown from them were again tested for presence or absence of this modifier in accordanc with the phenotype of the kernel from which the plant arose. These tests verified the presence of the modifier in those plants that were derived from the kernels showing an increased frequency of mutation and its absence in those plants that were derived from the kernels that exhibited the usual frequendy of mutation associated with the state of a_1^{m-1} present in the plant. They also showed that Spm was required for the modifier to be expressed. It was also possible to learn from these tests that the modifier undergoes transposition in somatic cells. This results in removal of it from some cells, and increase in its number in others. In one case, this resulted in its insertion into chromosome 9, and linkage of the modifier with Wx could be determined in plants having the modifier in this location. Removal from this location and insertion elesewhere coul also be followed. Detailed evidence for the statements given above cannot be included in this report. However, in order to indicate some of the methods used in obtaining this evidence, several of the tests will be outlined.

In the cross of plant 6889 to a plant that was homozygous for a_1, sh_2 and had no Spm, 12 plants derived from the variegated kernels showing the usual number of mutant spots (Spm, no modifier) were crossed by plants homozygous for a_1, sh2 and having no Spm, and also by plants homozygous for

a_1^{m-1}, (state), Sh_2 and having no Spm. The types of kernels on the ears these crosses produced are entered in A and B of table . Eight plants derived from the variegated kernels with an increased number of mutant spots (Spm plus modifier) were also used in crosses of the same type. The types of kernels appearing on the ears resulting from the c ross with the plants homozygous for a_1 and sh_2 are entered in C of table . Because the kernels on the ears produced by the cross with the a_1^{m-1} Sh_2 no Spm tester plants have different states of a_1^{m-1} in them that would require additional categories of kernel types in the table, they have been excluded from it.

7267
Cultures

A. $a_1^{m1}Sh_2 / a_1 sh_2$; Spm; no modifier ♀ × $a_1 sh_2 / a_1 sh_2$; no Spm, no modifier ♂
B. " " " × $a_1^{m1}Sh_2 / a_1^{m1}Sh_2$ " " ♂
C. " " " ; modifier ♀ × $a_1 sh_2 / a_1 sh_2$; no Spm, no modifier ♂

	number of plants tested	number of ears	germinal mutants	uniformly dark pale		areas of deep color in colorless background. (see figure)		Very many areas of deep colored in colorless background		Colorless		Totals
				no Spm		Spm, no Modifier		Spm, modifier				
	7267		Sh_2	Sh_2	sh_2	Sh_2	sh_2	Sh_2	sh_2	Sh_2	sh_2	
A	C 3-7 D 1-3,5 1) 8	11	5	557	3	592	1	0	0	12	1141	2311
	2) Tiller C-7	1	0	28	0	169	1	0	0	0	206	404
	3) tiller D-5	1	0	95	0	0	0	0	0	0	114	209
B.	7267 C 1-7, D 1- 1) 11 1 Spm	11	4	2013	–	1995	–	0	–	0	–	4012
	2) D-4 1 2 Spm	1	2	66	–	253	–	0	–	0	–	321
C	1) (1 Spm; 1 modifier) A-3 B-1 B-5 3	6	4	372	0	165	0	187	1	3	729	1461
	A-3 E-2 B-11 2) 1 Spm, 2 modifiers 2	2	2	86	0	30	0	94	0	1	200	413

Durand

present in some of its gametes. Following introduction of the a_1^{m-1} locus from the male parent, the presence of Spm in those kernels that received it from the female parent should be revealed by the appearance in them of small deeply pigmented spots in a colorless background due to activation of the a_1^{m-1} locus by the Spm element. In those kernels that did not receive Spm, the aleurone layer should be uniformly pigmented. Among the 30 plants derived from the colorless, sh_2, Y class of kernels, it could be determined on this basis that 15 had a single Spm element and 15 had no Spm. In 13 of the 15 plants that had Spm, linkage of it with Y was evident (A, table 2) but in the 2 remaining plants, no linkage of Spm with Y was noted (B, table 2) (The reason for the absence of linkage of Spm with Y in these 2 plants will be considered in the next section. It need only be mentioned here that this is not unexpected.) Among the 24 plants derived from the colorless, sh_2, y class of kernels, 6 had a single Spm element (C, table 2), and 18 had no Spm.

new ¶

In the above described test, the state of a_1^{m-1} present in the tester stock (pollen parent) was either that shown in - or - of figure 1. All of the kernels having Spm exhibited the pattern of variegation characteristic of the introduced state,-- small spots of deep pigmentation in a colorless background, and these spots were rather uniformly distributed over the aleurone layer. Also, all those that had no Spm were uniformly pigmented either darkly pigmented if state - had been introduced by the male parent, or lightly pigmented if state - had been so introduced. More than one fertile ear was produced by some of these plants. This made it possible to place on the silks of some of these additional ears pollen of plants in which Spm was considered to be absent but in which other states of a_1^{m-1} were present. This was done with plants having the states shown in -, -,-, and - of figure 1. It was found that if the element present in the pistillate parent had activated the state of a_1^{m-1} present in the tester stock, it would also activate each of these other states of a_1^{m-1}. However, the pattern of variegation that appeared in the kernels that received Spm was not the same as that given by the tester stocks. Instead, it was that which characterized the particular state of a_1^{m-1} that had been introduced by the pollen parent. That the activating element, nevertheless, was the same for each state could be shown in some of these tests by means of its linkage with Y and an illustration of this is given in D of table 2. ~~A more direct~~ other tests which show the activation of the different states of a_1^{m-1} by the same Spm element were conducted and the result of one of these ~~tests~~ is illustrated in figure 2. In this test, a variegated plant having the state of a_1^{m-1} shown in - of figure 1 was

was crossed by a plant in the Spm tester stock having the state shown in - of figure 1. Without exception, all kernels that exhibited the pattern of variegation characteristic of the state of a_1^{m-1} present in the female parent likewise exhibited the pattern of variegation characteristic of the state of a_1^{m-1} that was present in the male parent. The same element activated both states of a_1^{m-1}. Another type of test involved use of ~~pollen from a~~ plants that were homozygous for the standard recessive, a_1 and in which ~~the~~ one or more Spm ~~constitution~~ elements could be present ~~not be determined by phenotype of the plant~~. Pollen from one ~~such a~~ plant was distributed on ~~placed upon~~ the silks of ears of ~~a number~~ of non-variegated plants among which ~~a number of~~ different a_1^{m-1} states were represented ~~were represented~~. From each ~~such~~ test of this type the ratio ~~proportion~~ of variegated to non-variegated kernels was the same, regardless of the state of a_1^{m-1} that was present in the pistillate parent, and the type of ratio revealed ~~The proportion of these two classes of kernels~~ ~~indicated~~ the number of Spm elements that were present in the pollen parent. Again, if linkage of Spm to a given sensitive marker was expressed among the kernels on one ear, it was also expressed in all ears where this could be detected.

Phenotypes of kernels appearing on ears of plants having constitution shown in column 1 when pollen of plants homozygous for a_1^{m1}, sh_2, + no Spm + y was placed on silks of these ears.

Table 2

6663
6662

Phenotypes of kernels

Constitution of pistillate parent	No. of plants with given constitution	Uniformly pigmented (no Spm) Y	Uniformly pigmented (no Spm) y	Spots of deep pigmentation in colorless background (Spm present) Y	Spots of deep pigmentation in colorless background (Spm present) y	Total no. of kernels
A $a_1 sh_2/a_1 sh_2$ Y Spm/y +	13 plants	813	1467	1386	815	4481
B " " Y/y; 1 Spm	2 " (6665 G-16, " G-21)	96	97	126	116	435
C. " " y/y; 1 Spm	6 "	—	1260	—	1216	2476
D. $a_1^{m1} sh_2/a_1 sh_2$ Y Spm/y +	15 "	665	1156	1080	638	3539
E " " Y/y; 1 Spm	1 "	43	47	31	35	156
F " " Y/y; 2 Spm	1 "	45	58	119	115	369
G-(1) " " Y Spm/y + main ear		40	74	71	41	226
(2) " Y/y; 1 Spm, tiller ear		122	129	144	121	516
H. " " y/y; 1 Spm	8	—	864	—	852	1716
I $a_1 sh_2/a_1 sh_2$ Y Spm/y +	30	1366	2619	2472	1335	7792
J. " " y/y 1 Spm	17	—	3465	—	3281	6746
6863 (6665 G-21) K " " Y/y 1 Spm	4	477	500	455	462	1894
L. " " " Spm/Spm	2	3	4	259	281	547
6867 (6665 G-21) M. " " Y/y 1 Spm	15	1536	1664	1544	1654	6398
N $a_1^{m1} sh_2/a_1 sh_2$ Y Spm/y + (?)	1	68	92	82	61	303
O " " Y/y 2 Spm	1	82	75	203	201	561
6866 (6665 G-16) P. $a_1^{m1} sh_2/a_1 sh_2$ Y Spm/y + (?)	7	581	713	628	543	2466
Q " " Y/y 2 Spm	1	51	71	170	175	467
R. " " Y/y 3 Spm	1	16	15	95	110	236
S 6665 G-1 main $a_1^{m1} sh_2/a_1 sh_2$ Y Spm/y + main ear 6638 A-3		67	130	141	78	416
S-2 6665 G-1 tiller " " tiller ear 6701-2		60	140	122	91	413
S " "		—		—		

* a few somatic mutations not scored — too few.

Transposition of Spm -

1. Parent plant - 1Spm; progeny florets with no Spm 37.
2. " " - 1Spm - linked - " " cross with no Spm - Recombinants, + non-recombinant.
3. Differences in tillers of same plant - linked
4. " " sectors in same stalk - tests. Same ear

Ratios=

Plants from $a_1 \to A_1$ linked no Spm : plants from pale linked = Spm

Late transposition of Spm .

Ys wl y + a,d2 / a,d2	pale y	y	var y	y	
6665G-1[I] + 6638A-3	67	130	141	78	✓
" G(1)[I] + 6701-2	60	140	122	91	✓
" G(3)[I] no Spm " / " G(3) + 6638A-3. " } DD					
6630C-8 + 6701-2	—	294	—	0	✓
a,d2 y/y no Spm					
6666H-6 + 6638A-3	—	175	—	182	
" "[I] + 6704C-4 (a,mu/a,d2)	—	72		86	(164 a,d2

A. ♀	♂	pale sh_2	var. sh_2	Totals
$a_1 sh_2/a_1 sh_2$ 1 Spm	$a_1^{m1} sh_2/a_1^{m1} sh_2$ stock 5718 no Spm			
6861-1		229	174	
6861-7		139	148	

B. ♀	♂			
$a_1^{m1} sh_2/a_1^{m1} sh_2$ no Spm ×				
stock 5719A-1 (4 plants)	5861-1	788	779	
" " (5 ")	5861-7	988	988	

C.		colorless sh_2	var. sh_2	var. Sh_2	colorless Sh_2	totals
1) $a_1^{m1} Sh_2/a_1 sh_2$ no Spm ×	$a_1 sh_2/a_1 sh_2$ 1 Spm					
stock 5720 (6 plants)	5861-1	530	445	0	951	
2) 5 of 6 above plants ×	$a_1 sh_2/a_1 sh_2$ no Spm	741	0	0	795	
3) " " ×	$a_1 sh_2/a_1 sh_2$ 1 Spm					
(10 plants)	5861-7	886	798	1	1671	3356
" (8 of above 10 plants)	$a_1 sh_2/a_1 sh_2$ no Spm	1157	0	0	1177	2334

	pale	$a_1 \to A_1$
6861-1 × 6857-5 (stato −) 5718	229	174
6859-14 × 6861-1 (stato −) 5719A-1 — 4 plants	174	180
	245	247
	195	188
	174	164
	788	779

Totals

6899A (stato −) 5720 × 6861-1		Colorless Sh_2	$a_1 \to A_1 Sh_2$	$a_1 \to A_1 sh_2$	colorless sh_2
a_1 ... Sh_2/a_1 ... sh_2	A-3	86	74		152
	A-8	116	100		173
	A-9	86	68		154
	B-1	75	77		137
	B-4	60	62		152
	B-7	107	64		183
		530	445		951
			975		

6899A (8)t × $a_1 sh_2$ wo spm.	115	143
" (9)t × " "	119	103
" B (1)t " "	154	160
" B-(4)t × " "	234	256
" B-7 × " "	119	133
	741	795

	Pale Sh2	var. Sh2
6861-7 ♀ × 6857-5 (5718) (a Stato -)	139	148

Stato - 5719A-1 a_1^m/a_1^m × 6861-7 $a_1 sh_2/a_1 sh_2$	157	119
	206	288
	267	258
	247	217
	111	106
Totals	988	988

Stato 5720 $a_1^m sh_2/a_1 sh_2$ × 6861-7

No sum	Colorless Sh2	var Sh2	var sh2	colorless sh2	Totals
6899A-2	128	114	1	211	454
" A-4	107	80	0	196	383
" A-6	100	93	0	199	392
" A-7	120	117	0	228	465
" B-2	97	83	0	169	349
" B-5	100	110	0	196	406
" B-6	77	71	0	144	292
" B-8	24	21	0	60	105
" B-9	73	60	0	150	283
" B-10	60	49	0	118	227
Totals	886	798	1	1671	3356

6899 x $a_1 sh_2$ noSpm

	colchicine sh_2	colchicine sh_2	Totals
A 2	55	69	124
A 4	154	155	309
A 6	143	152	295
A 7	93	107	200
B-2	255	229	484
B-5	126	129	255
B-6	210	202	412
B-10	121	134	255
Totals	1157	1177	2334

A

Constitution of ♀	Constitution of ♂	Phenotypes of kernels: uniformly pale colored	A_1 dots in colorless background	Totals
$a_1 sh_2/a_1 sh_2$ 1 Spm [illegible]	$a_1^{m1} Sh_2/a_1^{m1} Sh_2$ no Spm stock 5718.			
Plant 6861-1		229	174	403
Plant 6861-7		139	148	287

B. $a_1^{m1} Sh_2/a_1^{m1} Sh_2$ (stock 5719A-1) no Spm ♀ × $a_1 sh_2/a_1 sh_2$ 1 Spm ♂; plants 6861-1 and 6861-7

			Totals
4 ♀ plants × 6861-1	788	779	1567
5 ♀ " × 6861-7	988	988	1976

C. $a_1^{m1} Sh_2$ (stock 5720) / $a_1 sh_2$ no Spm ♀ × $a_1 sh_2/a_1 sh_2$, no Spm ♂ and $a_1 sh_2/a_1 sh_2$ 1 Spm ♂

	Colorless Sh_2	areas of light pigmentation in colorless background Sh_2	areas of light pigmentation in colorless background sh_2	colorless sh_2	Total
6 ♀ plants × $a_1 sh_2/a_1 sh_2$ 1 Spm - Plant 6861-1	530	445	0	951	1926
5 of above plants × " " no Spm	741	0	0	795	1536
10 ♀ plants × " " 1 Spm ♂ Plant 6861-7	886	798	1	1671	3356
8 of above 10 plants × " " no Spm ♂	1157	0	0	1177	2334